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Author(s): Charles W. Fowler

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DENSITY DEPENDENCE AS RELATED TO LIFE HISTORY STRATEGY¹

CHARLES W. FOWLER

National Marine Mammal Laboratory, Seattle, Washington 98115 USA

Abstract. Both theory and empirical information support the conclusion that most density-dependent change occurs at high population levels (close to the carrying capacity) for species with life history strategies typical of large mammals. The reverse is true for species with life history strategies typical of insects and some fishes. Theoretical considerations that give rise to these conclusions involve natural selection and trophic dynamics. There is a large body of literature that contains descriptions of density dependence as based on empirical observations. These data, and the models used to represent them, indicate that species with high reproductive rates, short life-spans and populations held below the limits of environmental resources exhibit most density-dependent change at low population levels. Similar data for species with low reproductive rates, long life-spans and populations that are more limited by resources (large mammals in particular) indicate that most density-dependent changes in vital rates occur at levels of the population quite close to the carrying capacity.

Key words: density dependence; fish; insects; large mammals; life history strategies; natural selection; nonlinearity; population dynamics; r-K selection; trophic interactions.

INTRODUCTION

On theoretical grounds, Gilpin and Ayala (1973) have suggested that the population dynamics of various types of species should exhibit predictable patterns. They suggested that populations of vertebrates should exhibit their highest growth rates at levels closer to the carrying capacity than indicated by the logistic model. Gilpin et al. (1976) and Fowler et al. (1980:Appendix C) have described theory involving natural selection in which these types of dynamics are expected. Similar results are expected on the basis of trophic interactions (May 1973, Caughley 1976, 1979, Fowler et al. 1980:Appendix F). Other bases for expecting such results include competition and social dynamics (Gilpin and Ayala 1973) and the synergistic compounding of various regulatory mechanisms (Eberhardt 1977). The most important developments behind the theory related to such patterns in population dynamics involve: (1) natural selection, and (2) trophic dynamics.

To discuss the implications of natural selection in this context, it is helpful to visualize the specific rates associated with the patterns mentioned above. The linear specific, or per capita, rates $\left(\frac{dN}{dt} \frac{1}{N}\right)$ associated with the logistic equation imply a symmetric productivity curve, $\frac{dN}{dt} = f(N)$, as shown by B in Fig. 1. As the specific rates become nonlinear the population level that exhibits maximum growth $\left(\frac{dN}{dt}\right)$ shifts to one side or the other of $0.5 K$. In particular, the case in which most density-dependent

change occurs near the carrying capacity (C in Fig. 1) is the case where the growth curve $\left(\frac{dN}{dt} = f(N)\right)$ is skewed such that it reaches a maximum near K .

The specific rate of change $\left(\frac{dN}{dt} \frac{1}{N}\right)$ may be decomposed into birth and mortality rates. Fig. 2 shows hypothetical relationships between birth and survival rates and population size. Any point on the upper curves of both Figs. 2A and 2B corresponds to the rate expected as the mean reaction of the population size (N) to the various population levels shown on the abscissa. The curvilinearity of the relationships in Fig. 1 (curve C) and Fig. 2A is illustrative of cases where most density-dependent change occurs near the carrying capacity.

It is within the context of the relationships shown in Figs. 1 and 2 that the effects of natural selection may be considered. Populations of reproductive adults respond to their environment and its variability by exhibiting variability in population size. Some life history strategies represent more successful solutions to the problems of variability than others. Large-bodied species, for example, tend to have physiological strategies which help them resist such changes (Boyce 1978) and exhibit mean levels close to the limits established by environmental resources (K' in Fig. 2, Fowler et al. 1980:Appendix B). The variability about the long-term mean population level of such species is small (Fig. 2A) compared to that of species that are subject to higher levels of environmentally induced mortality (Fig. 2B), even though they may occupy the same space. In either case, females are under selective pressure to produce more offspring at reduced population levels. Females that increase their contribution to the population following a reduction below K will

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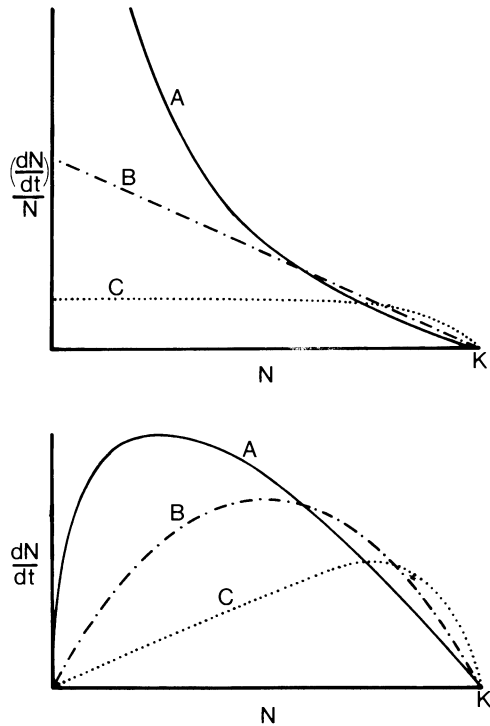


FIG. 1. A comparison of the population dynamics of three types of species. The upper graph shows specific rates (net growth rate per capita) and the lower shows the net rates of change, both as dependent on population size (N). The equilibrium population (K) has been forced to be the same for purposes of this comparison.

also contribute most to the genetic composition of succeeding generations. Such selective changes promote the existence of density dependence.

Natural selection of this type is expected to give rise to differences in the nature of density dependence as determined by the life history strategy of species distributed along the spectrum between the extremes outlined above and shown in Fig. 2. At the one extreme are those species with populations that exhibit low variability relative to their mean abundance as determined principally by resources (Fig. 2A). Although selective pressures may be very intensive at low levels for such species, they are not subjected to such selection simply because they very rarely occur at such low population levels (but see Estes 1979 for the effect of intervention by man). The energy and resources of such species can be devoted to the maintenance of mechanisms which contribute to low mortality. This results in low upper limits to the density-dependent responses that may occur at low densities (Figs. 1 [curve C], 2A). At the other extreme are species with highly variable populations that are held below the limits of their resources by the effect of the environment. Such species are more often subject to selection in which individuals that maintain a large capacity for contributing to future generations prevail. The result-

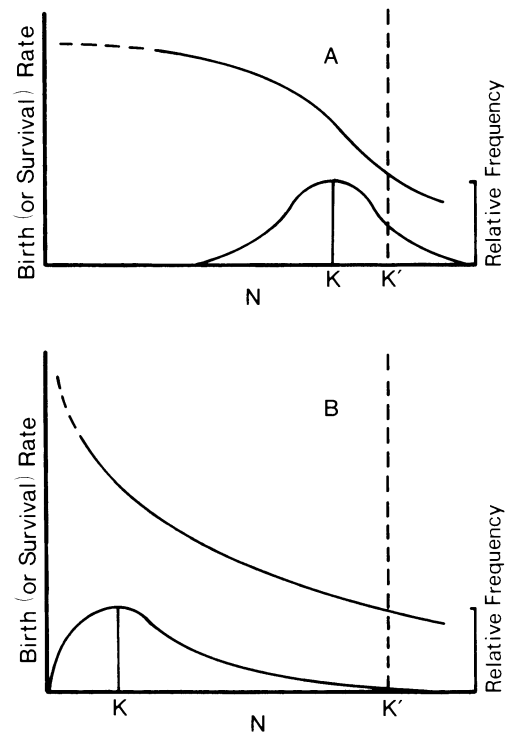


FIG. 2. A comparison of hypothetical relationships between birth (or survival) rates as dependent on population size (N) for two types of species. Species with long life spans and low reproductive rates and with populations limited to a great extent by resources are shown in (A). Species with high reproductive rates, short life spans and populations held below the limits set by resource levels are shown in (B). K' is the carrying capacity of each if determined by resources alone; K is the mean observed level resulting from the effect of finite resources in combination with environmental variability, predation and other environmental factors. The frequency distribution of observed population levels is shown (by the lower curve) as it would occur above and below K .

ing density dependence would be shown in Figs. 1 (curve A) and 2B. Populations of such species can dramatically increase their production if conditions are favorable.

The general conclusion of these evolutionary arguments is that large mammals and similar species are expected to show most of their density-dependent change at population levels quite close to the carrying capacity (Figs. 1 [curve C], 2A). At the other extreme, many insects and other short-lived species are expected to show most density dependence at lower population levels (Figs. 1 [curve A], 2B). Between these extremes intermediate cases will occur. Further detail regarding these and related arguments is presented in Gilpin et al. (1976) and Fowler et al. (1980:Appendix C).

As pointed out above, the effect of limitation by resources is involved in selective processes of importance to the nature of density dependence. Such an interaction may have a more short-term effect in pro-

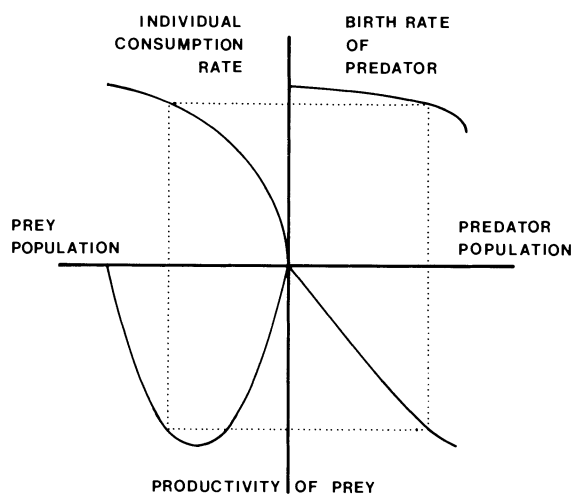


FIG. 3. Diagram of the density-dependent birth rate of a consuming population as it would be expected to change in response to density (upper right quadrant) as based on trophic interactions. All relationships are depicted as expected on the average or under equilibrium conditions. See text for details.

viding one of the mechanisms through which density dependence is exhibited. The effect of such trophic interactions on density dependence involves several components. These include the productivity (or growth) of the generalized prey population in direct or indirect response to its own population size, as well as the effect of the consumer population on the prey population. Also included are the reactions of the predator population to its prey base. These are summarized in Fig. 3 in which all four axes start at zero in the center and increase positively with increasing distance from the center.

As a predator population (axis on right of Fig. 3) is reduced, its consumption of prey (lower right quadrant) is reduced. The production of prey (bottom axis, expressed as a logistic function of the prey density on the left axis) which was being diverted to maintain predators is translated to growth of the prey population (left axis). The increased prey population results in an increased rate of consumption (functional response curve in upper left quadrant) by each predator. Because of the increased rate of consumption of resources by the predators, each individual has more to be devoted to birth and survival, especially of the young, within the predator population, and these rates increase (upper right quadrant). Further reduction of the predator population results in less marked increases in its birth rate because: (1) its functional response to prey density is limited (upper left quadrant), and (2) the prey population becomes more limited by its own resources or other predators and cannot continue to increase at the same rate (lower left quadrant).

As will be noted in the upper right quadrant of Fig. 3, there is a nonlinear relationship between the re-

sponse of rates characterizing the predator population and its own density. Thus, when birth and survival within a population are determined, at least in part, by the rate at which its individuals consume resources, most density-dependent change is again expected at higher population levels. Further details regarding this line of reasoning are presented in May (1973), Caughley (1970, 1976), and Fowler et al. (1980:Appendix F).

Most large-bodied mammals fall into two categories: herbivores and carnivores. Herbivore populations are predominantly regulated by resources (the primary producers upon which they depend, Fowler et al. 1980:Appendix B) and seem to be relatively free from regulatory effects of predators and diseases. As a result, large-mammal populations are expected to exhibit the type of dynamics shown in the upper right quadrant of Fig. 3. It can be shown that species regulated by higher level consumers are expected to show most change in density-dependent mortality at low population levels (Fowler 1980:Appendix F).

The arguments outlined above give rise to the hypotheses that: (1) large mammals and similar species show most of their density-dependent change at high population levels, and (2) species with highly variable populations, with high maximum rates of increase, exhibit most change at low levels. Although there is a great deal of confusion surrounding the terms, these two categories of species roughly correspond to the groups of species often referred to as the "K-selected" species and the "r-selected" species, respectively. In this paper, I evaluate the empirical information that relates to these tendencies and present a direct test of the first hypothesis.

METHODS

This study, which involves the comparison of the population dynamics of a large number of species, relies on information published by many individuals, most of whom conducted their work in the field or laboratory with populations of living animals. The data base provided by the collective published works of these researchers may be subjected to analysis through the fitting of models that result in curves such as those shown in Fig. 1. The resulting curves may then be compared to determine if the expected pattern is supported by the empirical information.

One such model is the Varley-Gradwell model (Varley and Gradwell 1968) where (in finite form):

$$\ln\left(\frac{N_t}{N_{t+1}}\right) = \ln a + b \ln N_t. \quad (1)$$

When rearranged this model takes the form:

$$\frac{N_{t+1} - N_t}{N_t} = \frac{1}{a} N_t^{-b} - 1 \quad (2)$$

which is nonlinear as shown by A in Fig. 1. The degree to which it is nonlinear is dependent on the parameter b . If we define N^* as the population level

at which $(N_{t+1} - N_t)$ reaches a maximum (as a function of N_t) and K as the equilibrium population (or the mean naturally occurring population as shown in Fig. 2) we see that the ratio (R) of these two values is:

$$R = \frac{N^*}{K} = (1 - b)^{1/b}. \quad (3)$$

Thus, this model shows a shift of the population which shows most rapid growth of (N^*) toward the carrying capacity (K) as b decreases. The ratio (R) is limited to $<1/e$ for this model since b cannot realistically be zero or less. As a result all data of which this model is representative will show dynamics typical of Fig. 2B.

Similar models which are useful for comparison include what is often referred to as the Graham-Schaefer model (Graham 1935, Schaefer 1954), the Beverton and Holt model (Beverton and Holt 1957), and the Ricker model (Ricker 1958):

Schaefer:

$$\frac{N_{t+1} - N_t}{N_t} = a - bN_t \quad (4)$$

Beverton and Holt:

$$\frac{N_{t+1} - N_t}{N_t} = \frac{1 - a - bN_t}{a + bN_t} \quad (5)$$

Ricker:

$$\frac{N_{t+1} - N_t}{N_t} = ae^{-bN_t} - 1. \quad (6)$$

These fisheries models also show dynamics in which $R = N^*/K$ is restricted to .5 or less, similar to A of Fig. 1. (Note that the parameters a and b change among models.)

Another model representing finite changes is as follows (see Allen 1976, Tillman 1978):

$$\frac{N_{t+1} - N_t}{N_t} = a - bN_t^c. \quad (7)$$

This model may be nonlinear with either positive or negative second derivatives as shown by Fig. 1 (C and A respectively). In the case of negative second derivatives, $R = N^*/K$ may approach the value 1.

Within the context of instantaneous models the logistic forms the point of reference (Fig. 1B):

$$\frac{dN}{dt} \frac{1}{N} = r \left(1 - \frac{N}{K} \right). \quad (8)$$

As is well known, $R = .5$ for this model. Other models with three parameters exhibit wide variability in R . These include the generalized growth model (Richards 1959) and a similar form used by Pella and Tomlinson (1969) and Gilpin et al. (1976). In the latter case, R may vary from 0 to 1.

The processes involved in birth and survival contribute to the dynamics of populations represented by

Eqs. 2 and 4 through 8. As such, birth and mortality rates can be examined independently. For example, an equation derived from Eq. 7 representing the birth rate would be:

$$B = a - bN^c. \quad (9)$$

A more simple form might be represented by a polynomial truncated to the second power:

$$B = a + bN - cN^2. \quad (10)$$

This can be used to fit empirical data and test for nonlinearity by examining its derivatives. A second derivative which is negative indicates dynamics of the type shown in Fig. 2A and line C in Fig. 1.

In this study Eq. 10 was chosen as a straightforward means to examine data representative of large mammals. The application of the other models as described in the general literature is used for an examination of the population dynamics of various species, particularly insects and fish.

Data showing density dependence in large mammals was collected from a variety of sources, particularly Fowler et al. (1980:Appendix B). Of the over 90 cases in which there is evidence of density dependence there are 27 cases for which the evidence is statistically significant and related to measured values of population size or density. The remainder of the cases are either anecdotal, based on samples which were too small to show significant changes, or involved changes in population size of unknown magnitude. The data used in this study involve birth rates, survival rates, and age at reproductive maturation.

By fitting Eq. 10 to the data from these studies, using least squares techniques, it was possible to determine an estimate of the second derivative of relationships such as those hypothesized in Fig. 2. These were then used to test the null hypothesis that one-half or more of the cases showing density-dependent change indicate that it is most pronounced at low population levels. Under this hypothesis the second derivatives of Eq. 10, when fit to the various groups of data, would either be evenly spread between negative and positive values (i.e., similar to the straight line in Fig. 1) or would show evidence of most change at low levels. This would be expressed as positive second derivatives for survival and birth, and negative second derivatives for age at maturation, as functions of population size or density.

Alternatively, a linear model fit to data for survival, for example, would support the hypothesis if it indicated an intercept >1 and would support the null hypothesis if the intercept were between 1 and 0. This is roughly equivalent to finding the tangent to a curvilinear relationship fit to the data and would indicate the nature of the curvilinearity.

Tests used in this analysis were based on the null hypothesis that, in naturally occurring populations, one-half or more of the cases show density-dependent

TABLE 1. A list of cases used to test for nonlinearity of density dependence in large mammals. See text for details.

| Species | Reference | Factor which changed | Data points | Evidence* |
|-----------------------------------------------------------------------|------------------------------------|------------------------------|-------------|-----------|
| Humans (<i>Homo sapiens</i>) | Paulus et al. (1979) | survival | 9 | + |
| Deer (<i>Odocoileus virginianus</i> and <i>Odocoileus hemionus</i>) | Teer et al. (1965) | ova per adult doe | 5 | + |
| | | embryos per yearling doe | 6 | + |
| | Hesselton et al. (1965) | embryos per adult doe | 5 | — |
| | | embryos per yearling doe | 5 | — |
| | O'Roke and Hamerstrom (1948) | fawns per doe | 13 | + |
| Elk (<i>Cervus canadensis</i>) | Swank (1958) | corpora lutea per doe | 4 | + |
| | Gross (1969) | calves per cow | 10 | + |
| | Fowler and Barmore (1979) | portion pregnant 2-yr-olds | 8 | + |
| Bison (<i>Bison bison</i>) | | juvenile survival | 10 | — |
| Longhorn cattle (<i>Bos taurus</i>) | Gross et al. (1973) | young per female | 19 | + |
| | | | | |
| Bighorn sheep (<i>Ovis canadensis</i>) | Gross et al. (1973) | young per female | 18 | + |
| | Geist (1971) | lambs per ewe | 11 | + |
| | Woodgerd (1964) | lambs per ewe | 8 | + |
| Soay sheep (<i>Ovis aries</i>) | | | | |
| | Grubb (1974) | juvenile survival | 8 | + |
| African buffalo (<i>Syncerus caffer</i>) | | adult survival | 7 | + |
| Grizzly bear (<i>Ursus arctos</i>) | Sinclair (1974) | adult survival | 7 | + |
| | McCullough (<i>in press</i>) | cubs per female | 12 | + |
| Wolves (<i>Canis lupus</i>) | Walters et al. (<i>in press</i>) | juvenile survival | 5 | + |
| Harp seals (<i>Pagophilus groenlandicus</i>) | Lett et al. (<i>in press</i>) | portion giving birth | 9 | + |
| | | age at reproductive maturity | 4 | — |
| | | juvenile survival | 6 | + |
| Northern fur seals (<i>Callorhinus ursinus</i>) | | | | |
| | Eberhardt (<i>in press</i>) | juvenile survival | 19 | + |
| Gray seals (<i>Halichoerus grypus</i>) | Coulson and Hickling (1964) | juvenile survival | 8 | + |
| Blue whales (<i>Balaenoptera musculus</i>) | Gambell (1975) | pregnancy rate | 6 | + |
| Fin whales (<i>Balaenoptera physalus</i>) | Gambell (1975) | pregnancy rate | 8 | + |
| Sei whales (<i>Balaenoptera borealis</i>) | Gambell (1975) | pregnancy rate | 6 | + |

* + = support of the hypothesis that large mammal populations tend to show nonlinearity in density dependence, with change most pronounced at high population levels; — = support of null hypothesis.

change which is most pronounced at low (<.5K) levels. Due to small samples, statistical tests were based directly on binomial probabilities rather than approximations.

The evaluation of species other than large mammals is based on roughly similar reviews of published studies, particularly that of Stubbs (1977). Stubbs' work must be reinterpreted on the basis of Eq. 3 and in light

of the restrictions of Eq. 1. Further trends are noted through an overall comparison of model types used for representing the dynamics of various groups as characterized by life history strategy.

RESULTS

Table 1 shows the sources of data used to determine the type of relationship observed for 27 cases in which

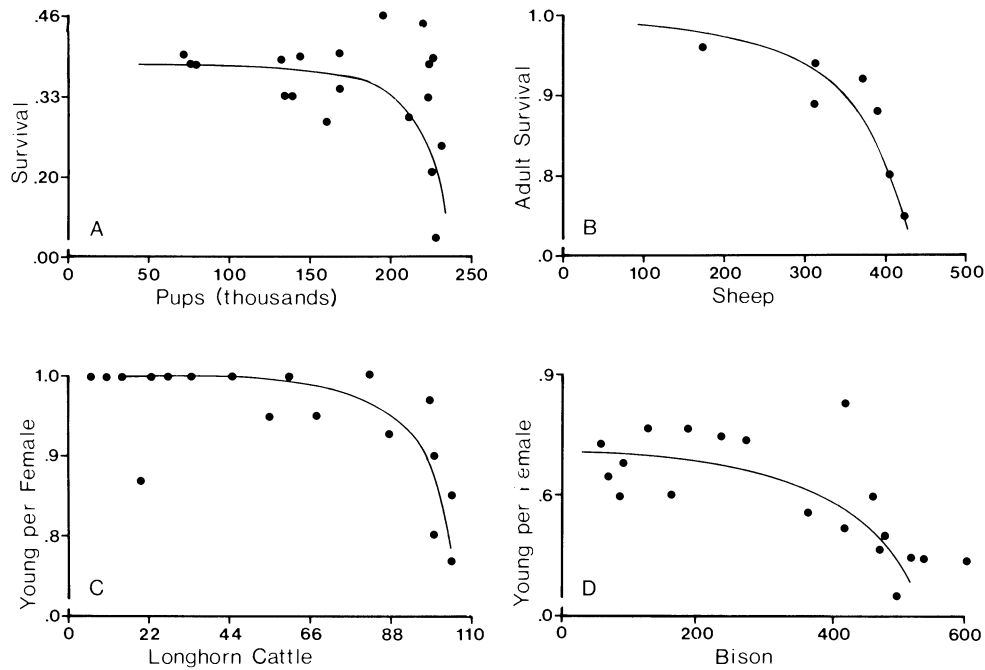


FIG. 4. Examples of nonlinear density-dependent changes in large mammal populations. A: the survival of northern fur seal (*Callorhinus ursinus*) pups as related to the number of pups born (Eberhardt, *in press*). B: The survival of adult Soay sheep (*Ovis aries*) as related to the population size found by Grubb (1974). C: The birth rate of feral longhorn cattle (*Bos taurus*) as related to density as reported by Gross et al. (1973). D: The birth rate of bison (*Bison bison*) as related to population size as reported by Gross et al. (1973).

density dependence has been shown to occur in large mammals. As will be noted, there are cases representative of the processes of birth, survival and maturation. The sample size is indicated for each case. Those cases which showed nonlinearity of the type shown in Fig. 1, curve C, are indicated by a (+); those which showed evidence of linearity or nonlinearity of the type shown in Fig. 1, curve A, are indicated by a (-). Fig. 4 shows examples of the data (plotted against density) included in Table 1.

Table 2 shows the results of tests applied to the information in Table 1. Of the 27 cases only 4 show evidence of nonlinearity in which most density-dependent change occurs at low levels. If the test is restricted to cases with larger sample sizes, the same trend is evident. In each subset of information (as shown in Table 2) the null hypothesis must be rejected. The probability of obtaining these samples if no pattern exists is $< .04$ in all cases. As shown in Fowler et al. (1980:Appendix C) it must be concluded that, in general, large mammals tend to show nonlinearity in density dependence where change is most pronounced at high population levels. The dynamics of such populations are expected to be of the type shown in Fig. 1C.

Similar tests can be conducted using data collected from a variety of species from the other end of the spectrum of body size and type of life history strategy.

Stubbs (1977) has analyzed data from 46 cases (comparable to the 27 cases in Table 1), 37 of which involve insects. She applied the Varley-Gradwell model (Eqs. 1 and 2) to data taken from the literature as representative of the processes of reproduction and mortality, especially the latter. As was indicated earlier, the parameter b in Eqs. 1 and 2 can be used to evaluate the degree to which density dependence is concentrated at the low end of the spectrum of population sizes.

In spite of the fact that $N^*/K = R$ (the ratio of the population's size at its theoretically maximum average growth rate to its natural mean population density) is restricted to $< 1/e$ for this model, Stubbs finds a relationship between b and the degree to which a species occupies a niche that involves a "permanent" versus a "temporary" habitat. Those from "permanent" habitats show low values of b and those from "temporary" habitats show larger (but more variable) mean values of b . Those species most likely to be called "r-strategists" tend to show dynamics which would be characterized by Fig. 1, curve A.

An appraisal of the general literature on population dynamics brings one to the conclusion that these trends have been a factor in the determination of the nature of population models in general. Although there has been considerable progress in the study of other invertebrates and vertebrates (e.g. see Tanner 1966), the most studied groups of animals have been fish (e.g.

TABLE 2. Statistical analysis of information in Table 1 based on binomial distribution with $H_0:p = .5$.

| Subset from Table 1 | Number of cases in subset | Number of cases supporting null hypothesis (see Table 1) | Probability of obtaining sample from population of cases where half or more would support null hypothesis |
|------------------------------|---------------------------|----------------------------------------------------------|-----------------------------------------------------------------------------------------------------------|
| All cases | 27 | 4 | <.0004 |
| Those with 8 points or more | 15 | 1 | <.0005 |
| Those with 10 points or more | 8 | 1 | <.04 |
| Those with 12 points or more | 5 | 0 | <.04 |

see McFadden 1977) and insects (e.g. see Stubbs 1977). The majority of the population models found in the literature are characterized by $R = N^*/K$ of .5 or less. These include models reviewed earlier as represented in Eqs. 2, 4, 5, 6, and 8. Most of these models originated in the study of fish and insects. Indeed, after examining a number of cases, mostly involving insects, Andrewartha and Birch (1954) conclude that a curvilinear relationship in which most change occurs at low levels is probably typical. On the other hand, Eq. 7 and the generalized growth model (with large value of the exponent) are more typical of work with large fish such as tuna, and especially large mammals (Fowler et al. 1980:Appendix C).

The conclusions of tests based on the information in Table 1, the interpretation of the work of Stubbs (1977) and the trends in application of general model types all support the existence of a pattern. This pattern involves the tendency of large-bodied (or “K-selected”) species to show most density-dependent change at high population levels. Conversely, insects, fish, and similar species tend to show most density-dependent changes at low population levels.

DISCUSSION

Eberhardt (1977) predicted the observed trends for large mammals in terms of the progressive expression of additional factors which resist further population growth as a population approaches equilibrium. Work by McCullough (1979), Raedeke (1979), and others as reviewed in Fowler et al. (1980:Appendix C) support this view. The growth of such populations at low levels may not be impeded to any significant extent by any single factor, while at levels close to the carrying capacity the synergistic and stronger effects of several factors produce an exaggerated resistance to further increase. In effect, each factor exhibits nonlinearity, some more so than others. Competition, social organization, genetic composition, coevolutionary inter-

actions, and spatial distribution are examples of such factors, all of which may have their own effects on the shape of the curves in Fig. 1.

Because of the potential effects of such factors, I have been purposely vague about ascribing the overall pattern to any particular cause-and-effect relationship. The pattern seems to be related to a general spectrum of life history strategies as they involve reproductive rates, longevity, body size, and population variability. The majority of insects and fish seem to show most of their density dependence at low population levels; large mammals tend to show the other extreme. Insofar as such a pattern is related to life history strategies it places population dynamics within the perspective of natural selection. Progress being made in relation to the evolution of life history strategies may be translated to conclusions concerning population dynamics.

The existence of a pattern, however, seems clear. Those whose work involves birds, small mammals or microorganisms should examine their literature for data comparable to that of Stubbs (1977) and that in Table 1. Details of the general picture can only become clear as more categories are subjected to similar analysis. With a more complete data base the patterns observed may be more critically examined in relation to various cause-and-effect relationships. Although it is possible to produce theoretically based guesses concerning the extent to which density-dependent change is concentrated at high population levels for large mammals (Fowler et al. 1980:Appendix F), further empirical work is needed to determine the degree to which this shift is determined by, or correlated with, life history parameters.

The implications of the pattern presented above need to be recognized. Important practical considerations relate to the understanding and management of populations as such activities are involved in the harvesting of resources, control of pests, and protection of endangered species. The stability of interspecific relationships as they influence the structure and function of ecosystems (and vice versa) should be viewed in light of these patterns.

Our views of the proper management and protection of large mammals, in particular, are in need of change. The management of marine mammals, for example, has often been based on models derived from work involving fisheries. In meeting requirements of the Marine Mammal Protection Act (MMPA, Public Law 92-522, 1972), for example, the Optimum Sustainable Population (defined in Federal Register 21 December 1976, 41FR55536) has been bounded on the high side by the carrying capacity and on the low side by the population giving rise to maximum net productivity. Historically, the lower bound has been close to .5K. Based on the evidence presented above, the Marine Mammal Protection Act requires protection for populations at all levels except those which are quite close

to the carrying capacity. Many populations of marine mammals are far below levels which would be most productive. It is likely that species such as the harp seal would be more productive if managed at higher population levels.

The productivity of big game populations is expected to be greatest at levels very near those which would be expected under natural (no harvest) conditions. Detailed work should define the relationship in each case but it is possible that deer, elk, antelope, and other big game populations will be most productive at levels which result in some degree of impact on their resources. In other words, range managers who define carrying capacity in terms of the quality of available forage may be in error both with respect to the equilibrium population and the level from which most production might be expected.

The detection of density dependence in large-mammal populations will be affected by the patterns characteristic of these types of populations. Measures of density dependence may depend on data collected from such a population fluctuating near the equilibrium with its natural environment. Populations of large mammals which have been reduced, even slightly, may exhibit little evidence of differences since there is a wide range of low levels over which little change may be expected. Given the statistical problems of evaluating vital rates, there is little chance of detecting significant changes over the lower levels of such populations. It is thus important that base level information be collected under natural conditions (at K in Fig. 1).

Finally, it is important to recognize the difference in the characteristics of the growth of populations which are subject to the different types of density dependence as shown in Fig. 1. Populations which grow from low levels will approach their equilibrium in different ways. Those which show most density dependence at low levels will grow most rapidly at low levels and approach their carrying capacity slowly. Populations of large mammals (and, if applicable, other K -selected species) will grow most rapidly as they reach levels quite close to the carrying capacity. This type of growth is exemplified by the exponential-like increase which characterizes the populations of several marine mammals (Chapman, *in press*). After undergoing the initial exponential growth the populations are expected to either "overshoot" their carrying capacity or suffer a dramatic halt in growth as the population becomes abruptly limited by its interactions with its environment (as shown for white-tailed deer by McCullough [1979]). The possibility that time lags will cause populations to increase well beyond ultimate mean levels is great in such cases. These types of species have not evolved under conditions of severe and frequent reductions. As a result, there are few mechanisms that operate to prevent excessive growth and the eruptions which seem to characterize the pop-

ulations of many introduced species of large mammals (Caughley 1970). How these principles relate to the human population is unclear due to our technologically and socially complex nature. However, humans are large mammals and also show evidence of density dependence (Paulus et al. 1979) typical of that expected for large mammals. Humans were the subject of some of the earliest work in which these types of dynamics were described (Farr 1843).

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